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Shrub growth and expansion in the Arctic tundra: an assessment of controlling factors using an evidence-based approach

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Abstract

Woody shrubs have increased in biomass and expanded into new areas throughout the Pan-Arctic tundra biome in the last decades, which has been linked to a biome-wide observed increase in productivity. Experimental, observational, and socio-ecological research suggests that air temperature – and to a lesser degree precipitation – trends have been the predominant drivers of this change. However, a progressive decoupling of these drivers from Arctic vegetation productivity has been reported, and since 2010, vegetation productivity has also been declining. We created a protocol to (a) identify the suite of controls that may be operating on shrub growth and expansion, and (b) characterise the evidence base for controls on Arctic shrub growth and expansion. We found evidence for a suite of 23 proximal controls that operate directly on shrub growth and expansion; the evidence base focused predominantly on just four controls (air temperature, soil moisture, herbivory, and snow dynamics). 65% of evidence was generated in the warmest tundra climes, while 24% was from only one of 28 floristic sectors. Temporal limitations beyond 10 years existed for most controls, while the use of space-for-time approaches was high, with 14% of the evidence derived via experimental approaches. The findings suggest the current evidence base is not sufficiently robust or comprehensive at present to answer key questions of Pan-Arctic shrub change. We suggest future directions that could strengthen the evidence, and lead to an understanding of the key mechanisms driving changes in Arctic shrub environments.

1. Introduction

The Arctic tundra biome provides essential regulatory effects to global climate, in particular albedo (Juszak et al 2014), storage of organic carbon in its living biomass (Nauta et al 2014), and permafrost dynamics (Blok et al 2010). Over at least the last three decades, changes in vegetation composition

have occurred that have significant consequences for the regulatory capability of tundra environments. Specifically, the ability of woody shrub species to produce biomass has increased, leading to shrubs of greater maximum height (Epstein et al 2012). Spatial expansion has also occurred: latitudinal ‘shrublines’ have advanced (Myers-Smith and Hick 2017), and new recruitment has enabled progressive filling of patchy landscapes (Tape et al 2006; Myers-Smith et al 2011; Frost, & Epstein 2014), both at the expense of mosses and lichens (Elmendorf et al 2012b). Such ‘**shrubification**’ has been a Pan-Arctic trend since the 1980s, supported by data from experimental plots (Elmendorf et al 2012a), remote sensing and repeat photography (Sturm et al 2001; Walker et al 2006; Epstein et al 2012; Frost, & Epstein 2014; Tape et al 2012; Tremblay et al 2012), dendrochronologies (Macias-Fauria et al 2012; Forbes et al 2010), and indigenous knowledge (Cuerrier et al 2015; Henry et al 2012; Forbes et al 2009).

Air temperature and growing season lengths have increased in tundra ecosystems more than at lower latitudes, due to positive feedbacks that snow and ice (both on land and at sea) have with climate (Serreze, & Barry 2011). Shrubification can be attributed primarily to air temperature changes (Myers-Smith et al 2015), and to a lesser extent soil moisture (Myers-Smith et al 2015; Ackerman et al 2017), although shrub responses are heterogeneous. Data from the International Tundra Experiment (ITEX) long-term plot network demonstrates regional differences in the responses of tundra vegetation to summer air temperatures (Elmendorf et al 2012a). Similarly, shrub ring chronologies indicate heterogeneous long-term responses to mean summer temperature, with maximum sensitivity in warmer and wetter tundra sites (Myers-Smith et al 2015). The observed heterogeneity suggests that other processes are important in controlling shrubification trends.

Shrubification has been linked to satellite-derived observations of widespread ‘**greening**’ (increases in vegetation productivity, as measured by the Normalised Difference Vegetation Index – NDVI). Recently, the NDVI index has shown widespread negative trends across the Arctic tundra for the first time in decades (Epstein et al 2015; Ju and Masek 2016). NDVI has been demonstrated as a correlative proxy for shrubification (e.g. Forbes et al 2010), but predictions based on NDVI assume that (a) correlations between plot-scale productivity and NDVI holds across Arctic regions, despite local-scale factors introducing uncertainty (Jorgenson et al 2015), and (b) the relationship holds under future conditions (e.g. increased landscape shrub biomass). Recognising these uncertainties, the recent negative NDVI trends could be driven by complex environmental controls on shrubs beyond simple temperature metrics, such climatic extremes, and/or discrete disturbance events (Phoenix and Bjerke 2016). A progressive decline in the relationship between air temperature and NDVI since 1982 (Piao et al 2014; Kremers et al 2015) further supports the role of controls beyond air temperature.

Rapidly increasing air temperatures or increased growing season lengths appear responsible for shrubification trends, but with significant roles for other controls that contribute to heterogeneity in shrub-temperature responses. Without a robust assessment of these controls, one cannot ascertain their relative importance, the adequacy of current study designs, or the evidence required to reveal mechanisms driving shrubification processes. We conducted an evaluation of the current evidence base to answer the following questions:

1. What are the suite of controls that may act upon shrub growth and expansion in the Arctic tundra?
2. Do study designs take account of controls to shrubification and the mechanisms that may drive them, and are there spatial gaps in the evidence base that may limit our ability to detect their significance?
3. Do study designs take account of temporal characteristics sufficiently comprehensively to enable inferences to be drawn about likely mechanisms?

2. Methods

2.1. Protocol

To establish the controls that may be operating on Arctic shrub growth and expansion, the quantitative evidence base for each control, and gaps in current research directions, we systematically mapped recently published literature (full protocol in *Appendix A*). Briefly, we searched the online database Web of Science Core Collection for “topic= Arctic AND Shrub*”, limited to publication years January 2012-January 2017. The following inclusion criteria were then applied:

- 1. Shrub Response.** The study carried out statistical analysis within which at least one direct measure of shrub growth or expansion was used as a response variable (see *Appendix A*).
- 2. Control.** Within the statistical test(s), an environmental control external to the shrub was used as a predictor to test against shrub response(s) identified in 1.
- 3. Location.** At least one site for which the statistical test was completed must occur within the Arctic tundra. We defined the Arctic tundra as any land north of the Arctic treeline (Walker et al 2002) and ‘Oro-Arctic’ areas (Virtanen et al 2016).

For each included source, we identified every environmental control used as a predictor, at every independent site. The many-to-many relationship between sources, controls, and sites was multiplied out to form source-control-site data points, hereafter referred to as **evidence points**.

2.1.1 Delineation of Methodologies

Methodology was characterised for each evidence point as non-experimental or experimental, then into subclasses depending on temporal characteristics. Following best practice in evidence synthesis (Collaboration for Environmental Evidence 2013), we characterised the data used within statistical analyses and not the data collected. For non-experimental evidence, **observational** controls had measurements taken through time to form a time-series of two or more time points. **Spatial gradients** used multiple measurements across space to substitute for time, while **chronosequences** attributed such variation across space to specific previous times to form a retrospective time-sequence. For environmental controls that had been manipulated, we defined four broadly distinct forms of experimental design based on the temporal nature of the data used within statistical analysis:

- (i) A **time-series factorial** was defined as an experiment in which measurements of both the environmental control and shrub response(s) were taken through time, and included in statistical analysis.
- (ii) A **response-only factorial** only included time-series for the response variable, with no predictor time-series.
- (iii) A **non-temporal factorial** contrasted the effect of a manipulation with a control plot, but no time series was present. For example, a nutrient addition experiment that tests for an effect on budding date after 18 years, with no ‘before’ point, and using differences between control and manipulation plots as a substitution for time, would fit this category.
- (iv) An **experimental chronosequence** used multiple plots through space with varying treatment lengths to assess the role of treatment on shrub response(s).

2.2. Classification of Controls

We classified the environmental controls found in the evidence base into two major categories – **ultimate** and **proximal** – to provide scope and rigour to the systematic analysis via this underlying framework (*Figure 1*). **Proximal controls** are defined as environmental state parameters that directly impact the ability of a shrub individual to increase in biomass, reproduce or establish, without the need for any intermediate environmental properties (e.g. soil moisture, fire). Proximal controls provide the minimal degree of complexity from which to characterise the underlying mechanisms controlling shrub growth and expansion. Where a proxy measure was used that could be directly attributed to a proximal control (e.g. thaw degree days, for ice and frost), this was included as an evidence point for the proximal control (all proxy measures listed in *Table A1*). Proximal controls are driven ultimately by further environmental properties that influence their occurrence in space and time (**ultimate controls**), such as the role of sea ice on local air temperature, but without support for any direct mechanistic relationship to shrub performance. Shrub traits (e.g. leaf size and properties, reproductive strategy, wood and vessel structure, metabolic adaptations, growth form, species-related

symbiotic relations, etc.) are significant determinants of plant-environment interactions, and can vary between genera, species, populations, ecotypes, and functional type (Chapin et al 1996). As we did not consider effect sizes in this analysis, we do not formally characterise internal controls here, and leave this for discussion and as a future avenue for research.

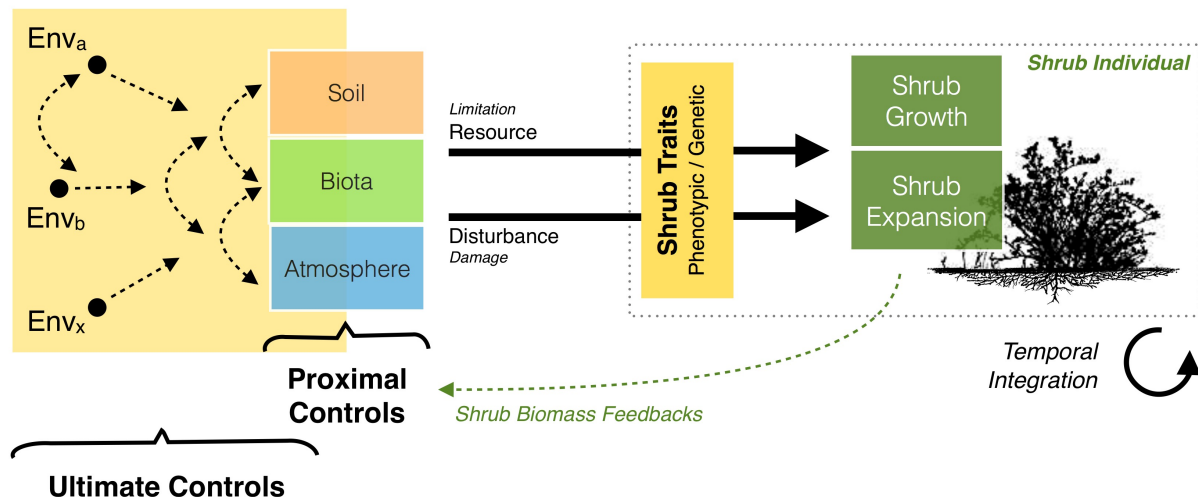


Figure 1 Conceptual overview of the framework used for the analysis. **Proximal controls** are state parameters that directly influence the performance of shrub individuals, without any intermediary role of other environmental parameters. These controls may be resources that can become limiting (e.g. soil moisture, nutrients), or disturbance drivers that can cause damage (e.g. gall mites, storm damage). The effectiveness of proximal controls is mediated by **shrub traits** (leaf size and properties, reproductive strategy, wood and vessel structure, metabolic adaptations, growth form, species-related symbiotic relations). The occurrence of proximal controls depends on additional environmental parameters – **ultimate controls** (Env_a , Env_b ... Env_x).

2.3. Analysis of Spatial Characteristics

To assess the degree to which the evidence points were spatially clustered or dispersed, we computed spatial autocorrelation using the Global Moran's I statistic (using an inverse distance spatial relationship over Euclidean distance). This approach was additionally utilised to identify spatial clustering for control categories, controls, and experimental designs. To identify specific hotspots of evidence production, we calculated the Getis-Ord G_i^* statistic (Getis and Ord 1992).

To identify research gaps in terms of broad environmental / ecological variability, we computed intersections between available Pan-Arctic layers and all evidence points, calculating Getis-Ord G_i^* for each resultant landscape component:

- for **climatic gradients**, we used bioclimate subzones, as defined in the Circumpolar Arctic Vegetation Map (CAVM)(Walker et al 2005);
- for **plant functional forms**, we used the Arctic physiognomic classification from the CAVM (Walker et al 2005), which reflects variability in above-ground ecosystem structure; and

c) for **biodiversity**, we used Arctic floristic groups and sectors (Elvebakk et al 1999; Yurtsev 1994), which represent broad patterns of plant species diversity (occurring due to regional differences in glacial and landscape history).

3. Results

135 of the 432 sources identified met the inclusions criteria and were included in the final analysis. We found 1,140 source-control-site evidence points reported during the period January 2012 – January 2017 (inclusive), derived from the 135 sources.

3.1 Suite of Controls

We identified 23 proximal controls (1,029 evidence points), presented in **Table 1**. Despite the range of potential proximal controls, there was predominant focus on just five: air temperature (including mean, maximum, minimum, above-freezing mean, growing degree days, and diurnal regional temperature proxies - 429 evidence points, or 41.69% of all proximal evidence points), soil moisture (including precipitation mean and sum, groundwater level, water track presence, and soil drainage proxies- 263, 25.56%), active layer depth (124, 12.05%), and to a lesser extent herbivory (66, 6.41%), and snow depth / cover (including snow-free date - 37, 3.56%). We also identified analysis of 24 ultimate controls within the evidence base, outlined in **Table 2**.

Table 1 Proximal controls to Arctic shrub growth / expansion assessed within the evidence base (Jan. 2012 – Jan. 2017 inclusive).

Category	Control	Form / Duration Variants	
Plant/Atmosphere Interface	Air Temperature	Winter Warming Event	
	Atmospheric Carbon Dioxide Concentration		
	Fire	Occurrence, Burn Intensity	
	Humidity	-	
	Ice and Frost	Ice Encasement (Rain-on-Snow) Events	
	Insolation	UV-B, Photoperiod	
	Snow Depth / Cover	-	
Biotic Interactions	Fungal Infection	-	
	Herbivory (includes trampling and other biomass removal processes)	Bird, Mammal, Gall Mites, Leaf Miners, Defoliators, Other Invertebrates	
Soil	Surface Conditions	Cryoturbation	-
		Erosion	Aeolian, Thermo-Erosion
		Soil Stability	Thaw Slump
	Belowground Conditions	Active Layer Depth	-
		Acidity	-
		Soil Moisture	Drought, Flooding
		Soil Salinity	Saline Incursion

	Soil Temperature	-
	Soil Texture	
Belowground Resources	Organic Matter	-
	Mineral Content	-
	Nitrogen	-
	Phosphorus	-
	Potassium	-

Table 2 Ultimate controls utilised during the period Jan. 2012 – Jan. 2017.

Category	Ultimate Control(s)
Climatic teleconnections	Sea ice extent/concentration.
Glacial and Periglacial	Time since glacial retreat; blockfields; ice-wedge
Geomorphology	polygons; pingos; palsas; patterned ground; physiographic unit; thermokarst; water tracks.
Topography	Altitude; aspect; elevation; exposure; physiographic unit; slope
Ecosystem Structure	Plant functional forms; total above-ground biomass; canopy height; competitive intensity; distance from current shrub range.
Human Activity	Proximity to human infrastructure; replacement by human infrastructure.

3.2. Spatial Characteristics of the Evidence Base

Spatial analysis revealed areas of research focus, and spatial gaps (full results in Appendix A.2.3).

Analysis of the spatial structure of all evidence points revealed global clustering (*Moran's Index* = 0.237, $z = 2.13$, $p = 0.033$). Hotspot analysis indicated six significant ($p < 0.05$) hotspots of evidence production, centred in Alaska (Toolik Lake, Barrow, and Atkasuk), Alexandra Fiord (Canada), Endalen (Svalbard), and Abisko (Sweden).

Patterns of spatial clustering were significantly different between study designs, and controls (**Figure 2, Figure 3**). Clustering was greater for proximal control evidence points alone ($z = 2.43$, $p = 0.015$), with ultimate control evidence points displaying no significant clustering or dispersal, being widespread around the circumpolar Arctic. Experimental research was focused around long-term ITEX experimental plots at Toolik Lake (23 points), Daring Lake (13 points), Svalbard (14 points), and in the Fennoscandian Oro-Arctic (55 points). Only two experimental evidence points occurred in non-Fennoscandian Eurasia above the altitudinal treeline. There were no significant global patterns for any individual proximal control, or proximal control category, aside from the air-plant interface (clustering, $z = 3.85$, $p = 0.00$), and air temperature ($z = 2.11$, $p = 0.03$).

Spatial analysis identified evidence gaps when intersecting by environmental / vegetation variability:

- A. **Climatic Gradient.** Arctic climatic bands were not equally represented within the dataset. Evidence points were weighted to the low Arctic in bioclimate subzone E (**Figure 2 and 3**), the warmest of the Arctic's zonal bands. 64.84% of evidence points occurred in areas with > 9°C July temperatures: 37.46% of evidence points intersected subzone E, while 27.39% intersected Oro-Arctic regions (**Figure A4**). Only 121 evidence points (10.69%) occurred in Subzones A and B (the highest latitude and climatically harshest regions), where some prostrate shrubs (i.e. *Salix arctica*) occur.
- B. **Plant Functional Form.** The evidence base was clustered significantly into the 'tussock sedge, dwarf shrub, moss tundra' physiognomic unit, in which Toolik Lake is located (full results in Table A4).
- C. **Biodiversity.** For floristic diversity, significant clustering occurred within the 'Alaskan Tundra' sector of the Beringia group. This sector accounted for 33.5% of all evidence points, despite only being 3.96% of the total tundra area, and only one of 28 floristic regions. Outside these regions, we identified evidence gaps in areas for which there few of no evidence points. During this period, no results were published for six floristic sectors (10.5% tundra area): Anabar – Olenyek, East Chukotka, Kharaulakh, and Wrangell Island (Russia), Jan Mayen (Iceland), and North Beringian Islands (Alaska).

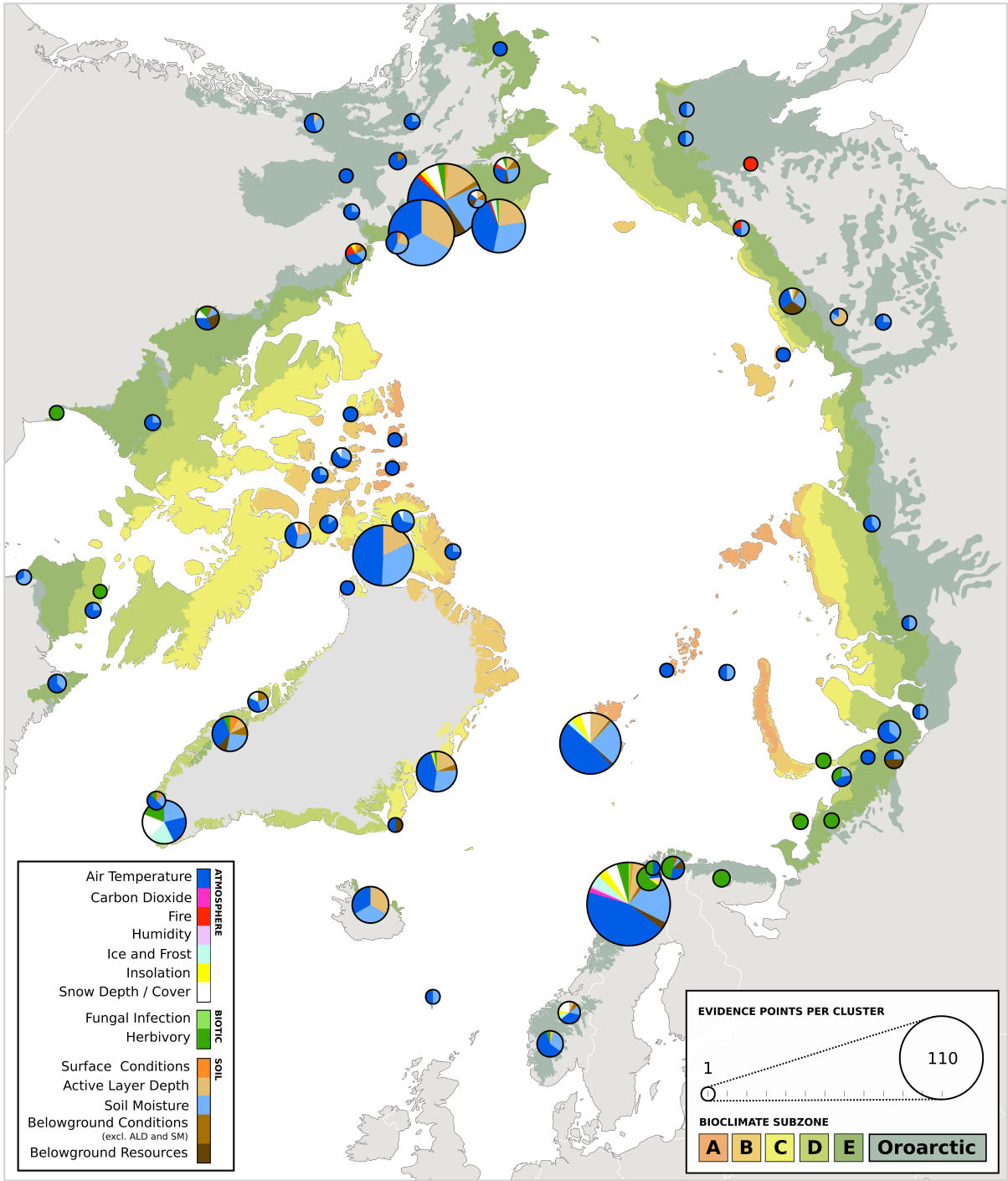


Figure 2 Pan-Arctic map showing evidence points generated for proximal controls on Arctic shrub growth and expansion (reported in peer-reviewed literature during the period 1 January 2012 – 31 January 2017). Each circle represents one location at which an evidence point was generated, or a regional cluster if more than one location occurred within 150km. Circle size represents the count of evidence points that occurred at the location. Pie segments represent a percentage of the evidence points at a location for each control type, represented by colour. Landmass colouring indicates bioclimatic subzone (Walker et al 2005), or Oro-Arctic (defined in *Section 2a*). Continental and Pan-Arctic evidence points are not represented in this figure. ALD = Active Layer Depth; SM = Soil Moisture.

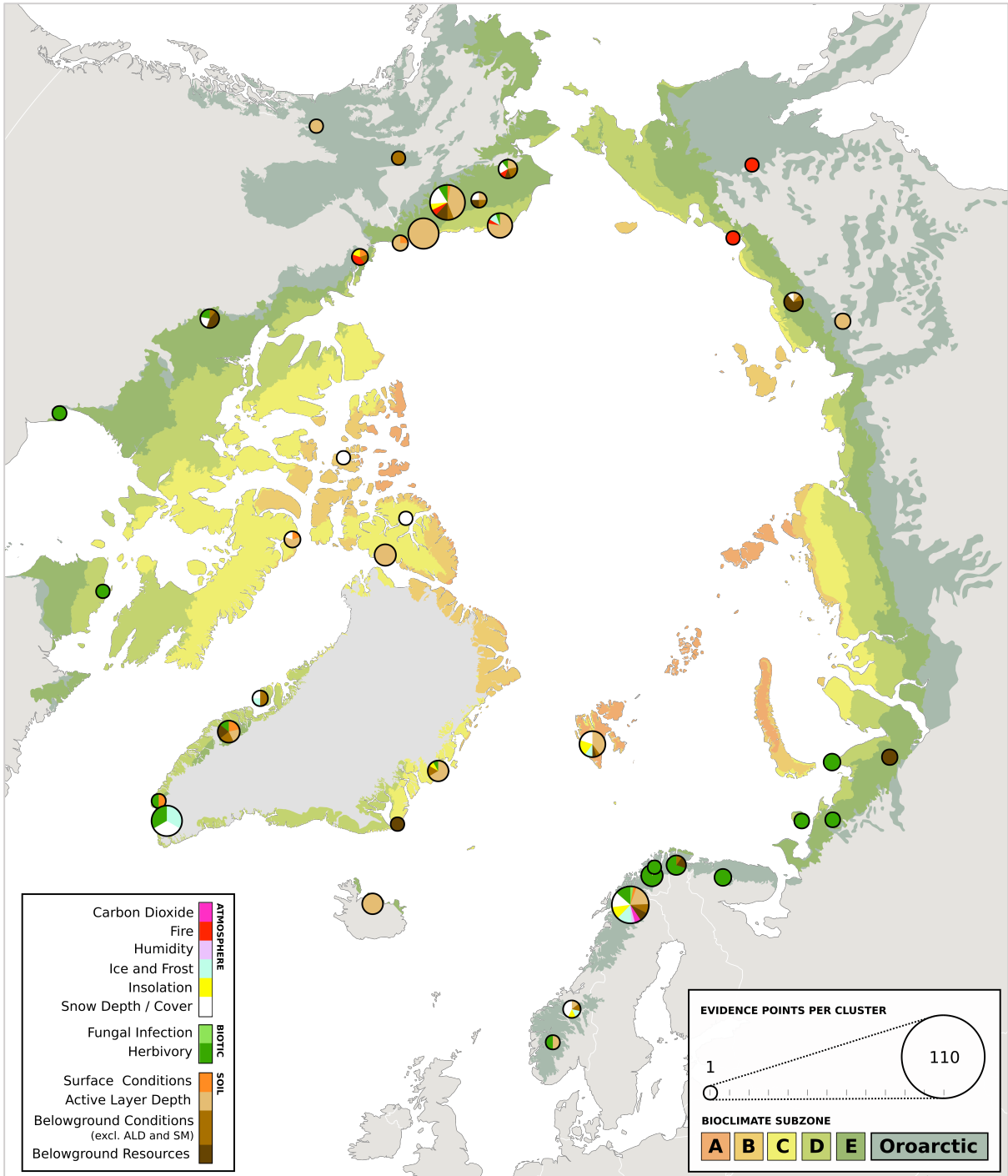


Figure 3 Pan-Arctic map showing evidence points generated for proximal controls on Arctic shrub growth and expansion (reported in peer-reviewed literature during the period 1 January 2012 – 31 January 2017), with air temperature and soil moisture sites removed from site pies to emphasise alternative controls. Each circle represents one location at which an evidence point was generated, or a regional cluster if more than one location occurred within 150km. Circle size represents the count of evidence points that occurred at the location. Pie segments represent a percentage of the evidence points at a location for each control type, represented by colour. Landmass colouring indicates bioclimatic subzone (Walker et al 2005), or Oro-Arctic (defined in *Section 2a*). Continental and Pan-Arctic evidence points are not represented in this figure. ALD = Active Layer Depth; SM = Soil Moisture.

3.3. Methodological and Temporal Characteristics of the Evidence Base

In total, 86% of evidence points were derived from observation, with 14% derived from experimental data. For proximal controls, we found the greatest use of spatial gradient approaches for air temperature (14%), herbivory (5%), and soil belowground conditions (soil moisture (40%), and active layer depth (28%)) predictors (**Figure 4A**). Spatial gradient evidence points constituted 40% of the total. Soil belowground resources were assessed for a median timespan of eight years, biotic interactions for ten years, air-plant interface controls for 29 years, soil belowground conditions for 50 years, and soil surface conditions for 240 years.

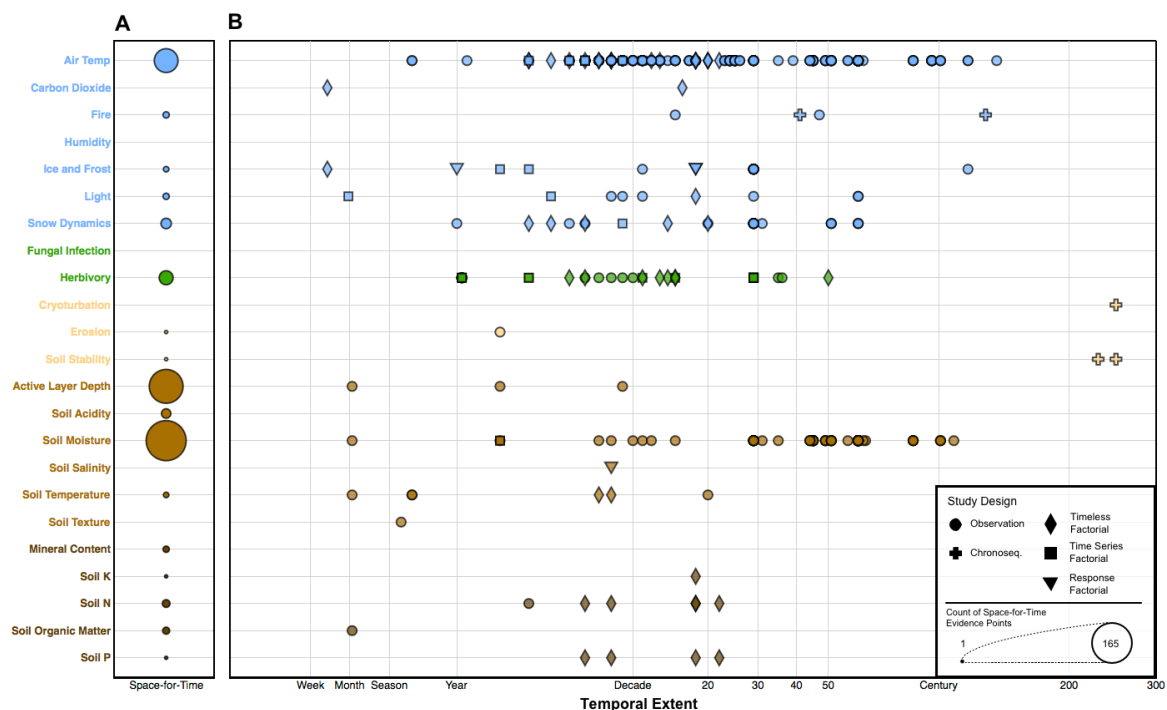


Figure 4A) Number of **space-for-time evidence points** per proximal control represented by circle size, excluding chronosequence approaches. **B)** Temporal extent of evidence points per proximal control (reported in peer-reviewed literature during the period 01 Jan 2012 – 31 Jan 2017). Temporal extent is defined as time series duration (observational and full factorial studies), time between newest and oldest phenomena (chronosequence), and length of prior manipulation before test ('non-temporal' factorial). Chronosequence is included here, despite being a space-for-time approach, as a concrete temporal extent is defined and used for analysis. Experimental design classifications are fully defined in Supplementary Material A.

Evidence was generally limited to no more than 25 years, aside from certain controls and study designs where long-term observational data could be obtained (**Figure 4B**). Decadal to centennial evidence was dominated by weather-station-derived proxy measures (coupled with dendroecological and repeat photography response variables): gridded, interpolated data products enabled numerous long-term studies of air temperature (proxy: regional air temperature), and soil moisture (proxy: regional precipitation). Space-for-time substitution was used widely, specifically for soil moisture, air temperature, and to a lesser extent herbivory, and snow dynamics. While observational evidence was

used for all proximal controls aside from atmospheric CO₂ and insolation (including UV-β), manipulations were limited to 13 out of the 23: air temperature, snow dynamics, herbivory, nutrient availability, ice formation, insolation, CO₂, and soil abiotic conditions. Experimental design and the resulting evidence was weighted towards the use of non-temporal analyses (**Figure 4B**). This was especially pronounced for certain controls: for soil macronutrients, 10 of 11 experimental analyses used this approach.

4. Discussion

4.1. Current Evidence Base

4.1.1 Suite of Controls

A predominant **focus on air temperature, soil moisture, and herbivory** controls suggests that other proximal controls – that may explain recent shrubification trends – are being overlooked. A scoping exercise (**Appendix A**) identified additional proximal controls that were not included in the compiled evidence base: abrasion by snow and ice crystals (Sonesson and Callaghan 1991), wind damage, microbial (Sedlacek et al 2014) and mycorrhizal (Deslippe and Simard 2011) associations, pollinators (Rich et al 2013), allelopathy (Bråthen et al 2010), soil micronutrients, and soil texture (Frost et al 2014). These proximal controls, alongside those that made a low proportion of the evidence base (atmospheric CO₂, insolation, cryoturbation, erosion (including aeolian and thermo-erosion), and fungal infection), may have been overlooked.

4.1.2 Spatial Gaps

Strong spatial clustering of the evidence base towards Alaska and Fennoscandia (**Figure 2**), as well as spatial gaps in the Eurasian Arctic (**Figure 5**), indicate that full spatial variability may not be captured for each proximal control. 65% of the evidence was generated within the warmest parts of the Arctic tundra biome, where summer (July) temperatures average above 9°C. Consequently, any controls and their mechanisms occurring exclusively, or with greater strength, in colder regions may be missed. Dominant processes driving shrubification vary between warmer tall shrub-dominated tundra (spatial infilling), and northernmost shrublines (increasing height and northward expansion). As these processes differ by biological mechanism, responses to controlling factors are likely different. The elevation gradient at Brooks Range has been used as a proxy for bioclimatic subzone, with elevation as a proxy for latitudinal space; however, the non-carbonate bedrock and acidic soils of the range do not account for the variability of plant functional forms and environmental conditions within higher latitude bioclimatic subzones.

Although shrubification trends appear to be driven by key species with Pan-Arctic distributions (*Betula nana*, *Salix* sp.), there are indications of regional genotypic variation in these, and other, shrub species (Abbott, & Brochmann 2003; Eidesen et al 2007; Eidesen et al 2013; Jørgensen et al 2012).

Similarly, there is evidence for significant phenotypic plasticity within shrub species in response to some proximal controls (Edwards et al 2005; Berner et al 2015), such as within-species spatial gradients from prostrate to erect growth forms. Significant focus of evidence in the ‘Alaskan Tundra’ floristic sector (Tkach et al 2010), and the Fennoscandian Oro-Arctic, may limit coverage of unique Eurasian ecotypes, species, and thus adaptations, resilience and/or vulnerabilities (**Figure 5**). Spatial focus on long-term ITEX plots at Toolik Lake and Daring Lake (Alaska, USA) has provided comprehensive evidence for moist, low shrub tundra environments; however, this habitat does not account for the breadth of tundra physiognomies (aside from tussock sedge, dwarf shrub, moss tundra’), where other mechanisms may be significant.

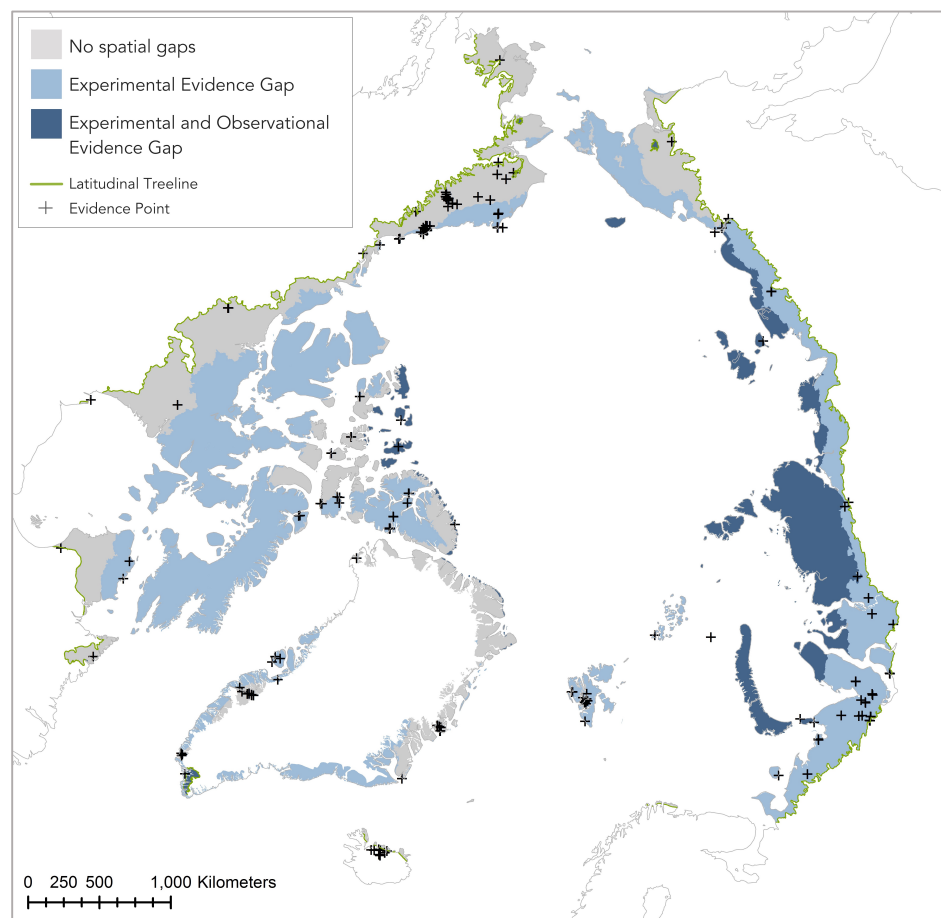


Figure 5 Map demonstrating regions of the Arctic for which there were evidence gaps during the period January 2012 to January 2017. The regional delineation displayed is bioclimatic subzone further split by floristic group. An evidence gap was defined as a bioclimate x floristic group region where there were five or less evidence points (equivalent to one or less point per year on average). Differentiation is made between evidence points derived from experimental evidence versus observational evidence (defined in 2.1.1).

4.1.3 Temporal Limitations

We noted temporal limitations to soil controls, where the extent of temporal evidence (aside from chronosequence) was generally limited to below 25 years (**Figure 4B**), while hypothesised drivers (e.g. changes in carbon and nitrogen cycling) may occur over decadal to centennial timescales. The

mechanisms through which controls may operate vary by their timescales, from diurnal to centennial timescales. The lower temporal resolutions for soil-based controls (**Appendix Figure A8**) also limits inference of within-season and inter-annual control variability, such as how seasonal variability may impact different life-stages (budding, flowering).

Without time series, one can establish the directionality of response, but not the functional form (linear, non-linear) of the mechanism(s) at work. As 42% of experimental evidence utilised non-temporal approaches, these evidence points cannot be used independently to ascertain temporal dynamics, but may only be useful when combined in meta-analyses (e.g. Elmendorf et al 2012b), assuming methodologies can be compared. Similarly, climatic gradients, and the Finland-Norway herbivory gradient, provided a large fraction of evidence. Such space-for-time substitution approaches do mask the rate and order of temporal processes, and have been empirically proven to overestimate the effects of air temperature on tundra shrub growth compared to experimental and observational data (Elmendorf et al 2015).

4.2. Applications and Limitations of our Approach.

One or more mechanism(s) may be responsible for the aggregate effects of a proximal control on shrub growth and expansion through space and time. In the context of global change, these mechanisms need characterisation if we aim at predicting future changes in shrub performance, habitat, and distribution. Our methods of metadata collection can be used as a tool to assess the suitability of the evidence base to support or refute possible mechanistic hypotheses. This approach is demonstrated for soil nutrients in **Box 1**.

We acknowledge limitations in our approach. First, the evidence gap between the Eurasian and North-American Arctic represents a publication bias; our search strategy does not cover Russian-language or other non-English scientific literature: spatial gaps in Eurasia may therefore have been accentuated. Second, we did not attempt to characterise the importance and strength of proximal controlling factors (resource limitations and discrete events) in space and time, but only the nature of the recent evidence base. Third, as our aim was to characterise the current trends in, and direction, of research, our analysis only represents the most recent five years of research, while older research may display different research quantities and priorities. We extended our search protocol to cover past research, finding that our study analysed 37.5% of all research captured by the search criteria (**Appendix A.2.1**).

Box 1. Soil Nitrogen and Shrubification

Soil macronutrients – including nitrogen (N), phosphorus (P), and potassium (K) – are essential resources for plant survival and fitness. Their availability is spatially heterogeneous at all scales (CAVM Team 2003; Walker et al 2005; DeMarco et al 2011), as a result of geology, glacial history, landscape processes, abiotic microhabitats, and plant community composition. Nitrogen is one of the most limiting macronutrients to growth in high latitudes (Bobbink et al 2010). There are multiple hypotheses for trajectories of tundra N availability, including: (1) increasing N availability as elevated soil temperatures increase the efficiency of N-mineralising microbes (Sturm et al 2005); (2) sequestration of N into long-lived woody biomass, reducing plant-available N in soils over decadal to centennial timescales (Progressive Nitrogen Limitation – PNL) (Luo et al 2004); and (3) increasing anthropogenic N deposition (Bobbink et al 2010).

Elevated N increases shrub aboveground biomass and shrub cover, with combined N-P limitation occurring in certain locations (Zamin, & Grogan 2012). Evidence was limited to 25 years, which is not long enough to support or refute some shrub-N interactions such as PNL: short-term mechanisms can distort long-term (decadal to centennial) processes (Johnson 2006). Exclusive use of non-temporal experimental approaches (**Figure 4B**) limits our understanding of rates of change, providing only single measures of ‘length and strength of manipulation’ to elevated response. The predictors do not quantify soil bioavailable N, essential to infer starting conditions and stressing and limiting levels of N, nor its forms, essential for understanding mechanisms of uptake and their variability between taxa and environments (i.e. organic versus inorganic forms). Manipulations often do not reflect the rates of change hypothesised for bioavailable N, fertilising at levels beyond expected quantities and rates of change (Bouskill et al 2014).

Past and future trajectories of N, thus N-shrub interactions, may be determined with alternative methodologies. Spatial variability in N or shrub traits (mycorrhizal associates, N-use efficiency) may explain the differences in observed N limitation across space, requiring measures of N and shrubification beyond ITEx plots. Temporal data could allow partitioning of short- and long-term responses that are difficult to differentiate using non-temporal approaches. Ideally, time-series measurements of bioavailable N on the same timescales as shrub responses would enable researchers to characterise rates of change within and between years whilst accounting for background N variability. Such time series could be interrogated using statistical modelling techniques, to infer the model and parameters of N-dependent growth.

To reduce uncertainty and increase predictive capability of future shrubification trends, we require mechanistic rather than correlative understandings of the underlying processes. We suggest three key knowledge gaps that must be reduced to gain such an understanding:

1. **Spatio-Temporal Trends of Shrubification.** Properties beyond biomass and cover that receive lesser attention, such as phenology (Prevéy et al 2017), and advancing shrublines (Myers-Smith et al 2017), could be measured for enhanced clarity over Pan-Arctic shrubification trends.
2. **Effectiveness of Proximal Controls.** Study designs may be sought that can assess the effectiveness per-unit variability within controlling factors on the identified mechanisms of shrubification, within the present range of environmental variability.
3. **Past and Future Variability of Control(s).** Each proximal control will vary through time due to a suite of underlying ultimate controls. Establishment of variability for the recent period, over which shrubification has occurred, and linking this to effect sizes, could enable establishment of (a) controls that are varying over the recent period, and (b) controls that may be responsible for observed changes.

We suggest four methodological directions through which tundra ecologists could enhance their study designs to address the above knowledge gaps:

1. **Incorporation of Time Series,** to establish the directionality and functional forms of shrub responses to environmental controls.
2. **Direct Measurement of Proximal Controls.** Many factorial studies did not measure the environmental control being studied, but rather measured the size and rate of perturbation. These methods assume that there is a direct link between perturbation and control (e.g. addition of 5g nitrogen fertiliser raises bioavailable nitrogen by a linear quantity). Inference of mechanisms could be enhanced by measuring the proximal control(s) directly, for example using automatic continuous loggers rather than gridded climate products. For time series, this will require creative solutions to overcome control-specific difficulties. Soil belowground resources, for example nutrients, require measurements by field researchers, but new technologies should be sought to increase automatic data collection capabilities.
3. **Use of Environmental Archives.** Palaeo-ecological and palaeo-environmental data from environmental archives can provide long-term indications of shrub response and environmental control. Fossil pollen accumulation rate data could be modelled as shrub biomass response (Seppä et al 2009) to a range of proximal controls. For the long-term, dendroecological or pollen data could be coupled to long-term proxies of nutrient availability

(McLauchlan et al 2013), herbivory (Baker et al 2016), and/or local climate (Jeffers et al 2012), from sedimentary archives.

4. Mechanistic modelling. Modelling approaches can be used to test competing hypotheses regarding the mechanisms underpinning plant-environment and biotic interactions through time (Jeffers et al 2012) and across space (Damgaard et al 2016); however, these approaches were rarely used in the evidence base.

5. Conclusions

Whereas there is significant evidence for an important role of air temperature and precipitation as drivers of Arctic shrubification, our systematic approach identified 23 proximal controls (those operating directly on the individual shrub and potentially affecting its growth and/or expansion) reported between January 2012 and January 2017, spanning soil properties, biotic interactions, and the plant-atmosphere interface. The focus of shrubification research has prominently been on air temperature and precipitation, while evidence suggesting a progressively declining role of climate requires us to consider other potential controls. We found spatial gaps in the evidence for all proximal controls, with research concentrated in the warmest bioclimatic zones of the tundra, and spatial gaps in Western and Central Arctic Siberia. These regions of research concentration already have a high percentage of tall shrub cover, while regions in the intermediate-latitude tundra (bioclimatic subzones B-D) were sparsely covered.

There is a basic mechanistic understanding of many of the controls on tundra shrubification, mostly derived from experiments conducted in acidic, low shrub, low latitude tundra, where shrubs are already a major component of the vegetation. In comparison, there is little focus on the mechanisms of range expansion and northward dispersal, operating at the northernmost range limit. In the studies included here, we found limitations in the temporal extent and resolution of evidence used, although this varied considerably depending on the proximal control considered. Study designs were in general found to be insufficient for investigating the mechanistic relationship between controls and shrubification, due to frequent use of non-temporal approaches. Reliance on space-for-time and non-temporal approaches risks not accurately reflecting the true rate and order of processes operating within the system.

We identify three knowledge gaps and four recommendations that tundra ecologists can consider to enhance the value of their data and future research. If progress is to be made toward predicting future spatial-temporal shrubification trends, more emphasis must be placed on the mechanisms underpinning shrubification.

The map is available as an online visualisation at: <https://oxlel.github.io/evidencemaps/arcticshrub>.

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